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Experimental evidence for inherent Lévy search behaviour in foraging animals

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Recently, Lévy walks have been put forward as a new paradigm for animal search and many cases have been made for its presence in nature. However, it remains debated whether Lévy walks are an inherent behavioural strategy or emerge from the animal reacting to its habitat. Here, we demonstrate signatures of Lévy behaviour in the search movement of mud snails (*Hydrobia ulvae*) based on a novel, direct assessment of movement properties in an experimental set-up using different food distributions. Our experimental data uncovered clusters of small movement steps alternating with long moves independent of food encounter and landscape complexity. Moreover, size distributions of these clusters followed truncated power laws. These two findings are characteristic signatures of mechanisms underlying inherent Lévy-like movement. Thus, our study provides clear experimental evidence that such multi-scale movement is an inherent behaviour rather than resulting from the animal interacting with its environment.

1. Introduction

Many animal species move through differently structured landscapes searching for food. When food items are unperceivable, animals are assumed to follow specialized random search strategies in order to maximize foraging gain [1–4]. Going beyond the classical approaches based on Brownian motion [5], Lévy walks [6,7] have been put forward as a new movement paradigm for animals searching for rare, hard-to-find food items.

Lévy walks are a special case of multi-scale walks, composed of clusters of short movement steps and frequent turns (i.e. small-scale clusters of area-restricted search, ARS) alternating with long-distance displacements. The ratio of short versus long steps is scale invariant in Lévy walks, described by the power-law probability density function $P(x_i) \approx x_i^{-\mu}$, with x_i being the move length (displacement of consistent direction) and μ representing the power-law exponent, where $1 < \mu \leq 3$. To make a distinction between this mathematically strict Lévy foraging hypothesis and biological, Lévy-like movement that optimizes search, we introduce for the latter the term 'multi-scale search behaviour'.

Initial scepticism against Lévy walks in natural systems [8,9] and critics on methodology [10–12] have been overturned [13,14] (but see [15]), and many

studies now show convincingly that Lévy-like, multi-scale search behaviour is not only present in a wide range of extant animals and humans [16–24], but can even be found in trace fossil trails [25].

The greatest challenge, however, is to discover and understand the mechanisms that underlie such multi-scale search patterns [26,27]. On the one hand, it has been argued that the observed, long-tailed move length distributions that point to a Lévy walk can result from the interactions of animals with fractal-shaped landscape properties [8,28,29], obscuring underlying Brownian movement. This hypothesis, called the composite Brownian walk [28], presumes that ARS is triggered by encounter of food or food-rich patches. On the other hand, evidence is increasing that multi-scale, Lévy-like movement patterns are shaped by intrinsic behaviours, independent of environmental drivers [30–32].

Recent simulation studies and experiments have shown that multi-scale walks are optimal search (and foraging) strategies for a wide range of environmental conditions [13,20,30,33], including completely uniform, unstructured landscapes [31,34]. Timing of spontaneous behaviours, like flight turns in *Drosophila* [31], ambush waiting in marine predators [35] and activity dynamics of mice [36], as well as planned task cueing in humans [37], revealed Lévy walk characteristics without environmental feedback, indicating intrinsic control by the nervous system. In million-year-old fossil tracks, Lévy walks were suggested to have emerged from simple self-avoiding trails, again suggesting an intrinsic mechanism that has evolved as a natural adaptation [25]. A combination of intrinsic and extrinsic drivers of Lévy walk patterns was shown by copepods searching for mates [23]. They exhibited intrinsic multi-scale search patterns in the absence of chemical cues as well as if pheromone was present, but with increased power-law exponents leading to more localized movement in the latter case. However, most of those examples are behaviours less complex than foraging, and a simple approach to test for the presence of intrinsic, multi-scale movement as a foraging strategy still seems to be lacking [38].

To fill this gap, we followed an alternative approach and experimentally tested for the presence of intrinsic Lévy-like search behaviour using small animals, mud snails (*Hydrobia ulvae*), foraging within artificial landscapes of patches of diatoms, their main food. After investigating the snails' cognitive performance, we determined their movement characteristics in artificial landscapes with different degrees of food heterogeneity. First, we evaluated the hypothesis, characteristic of Lévy foraging behaviour, that ARS clusters would occur irrespective of the encounter of food. This hypothesis was contrasted against the alternative hypotheses that (i) ARS clusters would form only in response to food encounter, which is the premise underlying the composite Brownian walk, and that (ii) snails would move straight between food patches (ballistic search) [39,40]. Second, we tested if the ARS clusters showed a long-tailed size distribution irrespective of the landscape configuration. This would indicate a complex alternation mechanism of intensive and extensive search behaviour [41], and point to intrinsic multi-scale search behaviour.

2. Material and methods

(a) Experiments

We collected sediment, benthic diatoms and mud snails at two different intertidal mud flats—the Kapellebank in the Westerschelde estuary (51.45° N, 3.97° E) and Dortsman in the Oosterschelde (51.52° N, 4.02° E)—in The Netherlands. Before use in the laboratory, the muddy sediment was defaunated (freezing at −20°C for 2 days) and sieved (5 mm) to remove coarse particles. Snails were kept in an aerated container with a thin layer of mud, filtered seawater and cultured diatoms for food.

To set up foraging landscapes, we isolated and cultivated motile epipelic diatoms [42], one of the major components of mud snail diet [43]. The filtered diatom suspension was applied on defaunated mud in 30 × 45 cm plastic containers, and food patch patterns were created by using a mesh template of 1.5 × 1.5 cm grids. Mesh cells were filled with either diatom suspension or filtered seawater. The food density in the patches was very high (approx. 100 μg chlorophyll-*a* per gram sediment [44]) to avoid depletion. To allow the diatoms to grow, the containers were placed below red and white LED light with a 12 L : 12 D cycle and the temperature was set to 13°C.

After confirming the assumption of limited cognitive performance for our system (see electronic supplementary material), the main experiment was set up. We prepared containers of five different landscape types for the main experiments (performed 27 July 2010 to 6 September 2010). Two landscapes were homogeneous (bare mud or completely covered with diatoms) and three landscapes were prepared with 10% of its surface covered with diatoms in different levels of patchiness (see electronic supplementary material). The 'regular' landscape was constructed by arranging mesh cells completely regularly, which allowed for frequent food encounter. The 'random' landscape was created by placing the same amount of cells randomly. With the 'fractal' landscape, we intended to replicate the patchy character of the natural habitat of mud snails; it was created using the midpoint displacement algorithm [45].

Once the diatoms were well grown on the mud, the mesh cells were carefully taken off. The container was refilled with approximately 2 cm of filtered seawater, and placed away from the LED lights under a webcam (Logitech QuickCam 9000 Pro) that was outlined by two fluorescent lights, providing homogeneous light conditions. Before each experiment, nine naive snails (that had not been used for any experiment before) were starved for 1 h and marked with a small dot of yellow nail polish for track recognition. All snails were treated in the same way, so the tracks in our experiment reflect comparable conditions apart from the experimental treatments. Furthermore, our conclusions are likely to be generalizable to unmarked snails, as the movements of a small sample of snails without nail polish were similar (see electronic supplementary material), and hence the nail polish seems not to have notably affected the snails' movements. The snails were then placed on the landscape in three rows and three columns at equal distances from each other, and the camera was set to take a picture each 10 s to record their movement paths for 5 h. After this time, the experiment was finished and the snails were removed.

The position of each snail was digitized as x/y coordinates, additionally recording whether the position was on a food patch or not. For each landscape, we used four replicates. Each snail was only used once, so altogether we recorded the tracks of 180 individual snails. However, for one of the regular landscapes, the experiment failed (landscape pattern destroyed), so that we used the tracks of 171 snails only. Furthermore, due to burrowing behaviour some snails did not move. Others moved directly to the edges of the containers, where we truncated their tracks. For analysis, we selected only individual tracks that contained more than 50 steps ($n = 116$). The number of those tracks did not differ much between landscapes.

(b) Data analysis

For each individual, the regularly sampled snail tracks were aggregated into sequences of moves (i.e. quasi-linear track

segments at which the snail did not change direction). We used two segmentation methods: (i) a new approach that identifies direction reversals in single dimensions (one-dimensional method [46]) and (ii) a two-dimensional technique extracting segments where the snail turns less than a certain threshold angle [5]. This threshold was selected to minimize the autocorrelation of stepwise directions [17], in our case $45°$. We determined and compared move length distributions of the two datasets, both for the tracks pooled by landscape and for each individual separately, forestalling that Lévy walks might be apparent from pooling the movement of animals that perform Brownian walks with typical move lengths of different sizes [47].

To additionally explore the influence of food encounter on move lengths, each of the two sets of distributions was split into moves (partly) within and (completely) outside of food patches. Each distribution was then fitted to power-law, truncated power-law, exponential and hyperexponential ($k = 2$ or $k = 3$) distributions using maximum-likelihood methods [48]. We selected the best fit by means of Kolmogorov–Smirnov goodness of fit, G-tests and Akaike weights [49]. From the two-dimensional move lengths, characteristic scales s_i of hyperexponential distributions were calculated as $s_i = x_{min} + 1/\lambda_i$ [48] and compared with the mean free path (mean distance between two food patches) for each landscape type.

Before fitting, we determined the minimum and maximum value (x_{min} and x_{max}) for every set of move lengths. We calculated x_{min} by using a bilinear fit and selecting the change point, as has already been shown successfully [18]. For determining x_{max}, we applied statistical theory [50], depending on maximum-likelihood estimation and confidence intervals.

For testing the inherent multi-scale walk concept that animals alternate small and large steps irrespective of the external environment, we calculated clusters of small steps (ARS clusters) from the original tracks and compared their properties between landscapes. We used the Brownian bridge kernel method (BBKM) [51,52], defining a regular grid for the landscapes (100×100 units; short side of arena, 300 mm/snail size, 3 mm) in which the movement tracks were embedded and attributed a probability of animal presence to each cell (see the electronic supplementary material). Each track was separated into positions within and outside of ARS clusters by selecting a cut-off probability outline (from the 25–80% outlines [52]) that maximized the difference between average turning angles in and outside of ARS clusters.

For each ARS cluster (shaped by more than or equal to three snail positions), we determined its maximum width (i.e. the maximum distance between any pair of two points of the cluster), area covered by the minimum convex polygon and time the snail spent in the cluster. The BBKM also detects clusters of slow, straight movement. To avoid considering these as ARS clusters, for any further analyses we excluded clusters for which the ratio of cluster area and cluster maximum width was below 0.2. Distributions of cluster sizes with and without encounter of food were fitted to power-law, truncated power-law, exponential and hyperexponential distributions (similarly to move length distributions; see above).

To address the question of whether mud snails alter their movement strategy at food encounter, we analysed their reorientation behaviour when they encountered and later left a food patch. We compared the distributions of turning angles of two-dimensional moves between entry and exit of a food patch with randomly placed turns of similar temporal spacing.

Finally, we analysed the search efficiency of mud snails with a survival analysis [53] grouping the tracks of regular, random and fractal landscapes. The variable of interest was the estimated probability of encountering a food patch after leaving one; this was calculated as the inverse of time until food encounter. We only included encounters after a snail had the experience of

food encounter to avoid bias due to different initial positions and mean free paths in each of the landscapes. For each snail track, we selected trajectory fragments that started when the snail had left a food patch and ended (i) at the subsequent encounter of either the same or another food patch, (ii) when the snail left the container or (iii) when the experiment was terminated. The last fragment of each track is of type (ii) or (iii), therefore those segments were considered 'censored data'. This means that time until the next food encounter is assumed to be after leaving the container or after termination of the experiment, but unknown.

3. Results and discussion

(a) Fitting move length distributions

When accumulating the move lengths of all individual snails per landscape type, irrespective of whether obtained using the one- or two-dimensional method—summing to over 22 000 (one dimension) and 40 000 (two dimensions) analysed displacements—move length distributions were similar between the landscapes (figure 1a,b) and clearly showed fat tails (i.e. a high frequency of long displacements), which is indicative for Lévy-like search behaviour. However, our statistical analyses showed that the composite movement model consisting of three exponentials (figure 1c,d and table 1a) provided a superior fit over the other models, pointing at possible composite Brownian movement [28,48]. Yet very similar composite exponential fits of the two-dimensional move lengths, with similar characteristic scales (pairwise Wilcoxon tests $p > 0.7$; table 1a), were obtained for both the patchy and homogeneous landscapes. This undermines the basic assumption of ARS models like composite Brownian walks that environmental triggers drive switches between alternate movement modes [28,29,48]. Moreover, the movement scales as obtained from the composite exponential fits (table 1a) corresponded to snail size (2–3 mm), but did not match with any landscape features like the mean free path (regular: 78 mm; random: 88 mm; fractal: 155 mm). Thus, foraging strategies of mud snails seem to be inherently multi-scale and not solely determined by their environment. This goes into the direction of an earlier suggestion that multi-scale composite movement is an internal mechanism to approximate Lévy walks [54,55].

Furthermore, if fitting truncated power laws to the data, power-law exponents were in the range typical for Lévy walks ($1.5 \leq \mu \leq 2.5$), irrespective of whether movement occurred on or outside of food patches (table 1a and figure 1c–f; see electronic supplementary material). In the regular and random landscape, the scaling exponents were slightly larger ($2.4 \leq \mu \leq 2.6$), indicating that frequent food patch encounters truncated long moves [30]. These results held true for both sets of move length distributions and also when we took individual variation in movement characteristics into account (i.e. analysed individual tracks separately; see electronic supplementary material). If contrasting exponentials with (truncated) power laws, the majority of individual tracks were best fit by a (truncated) power law, but only for 45.7% of the individuals did the fit range over more than 1.5 orders of magnitude, allowing doubt about this method to infer strict Lévy search properties. Hence, the results of classical statistical analysis of move length distributions remained inconclusive and are open to different explanations, similar to what is found in other studies in animal search theory [10,48].
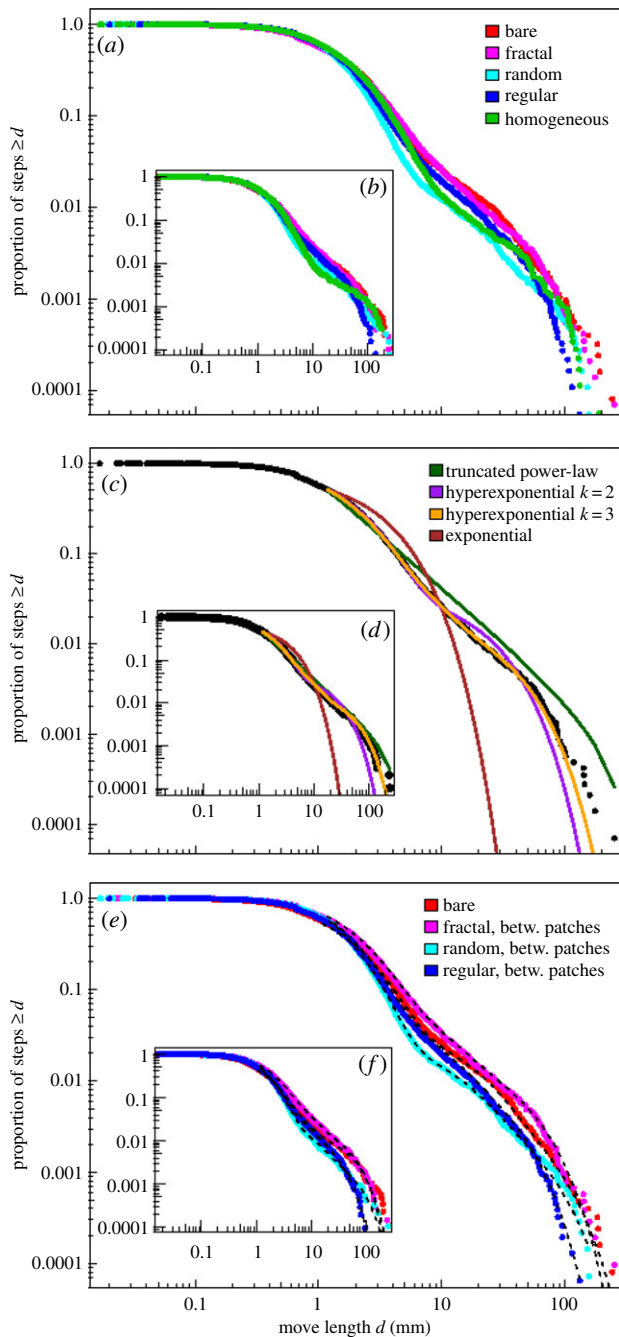
Figure 1. Cumulative move length distributions of mud snail tracks. From regularly sampled tracks, moves were determined as consecutive two-dimensional track segments with turning angles of less than 45° or as one-dimensional direction reversals. (a) Pooled distributions of two-dimensional move lengths and (b) one-dimensional move lengths in x-axis direction (y-axis similar, not shown) of individuals foraging in five different landscapes, showing similar patterns. They point to an inherent multi-scale movement strategy, being only slightly modified by food encounters. (c) Pooled two- and (d) one-dimensional x-axes (y-axis similar, not shown) move length distribution of snails in the fractal landscape with maximum-likelihood fits of exponential (simplest way of random movement), truncated power-law (indicating Lévy walks) and hyperexponential models (k = 2 and k = 3; recently proposed to stand for composite Brownian walks). The latter is favoured by AICs. (e) Pooled distributions of two- and (f) one-dimensional move lengths occurring only between food patches in four different landscapes. Dashed lines indicate the hyperexponential (k = 3) best fits to each of the distributions. Note that distributions did only slightly change shape compared with (a,b). (Online version in colour.)

(b) Area-restricted search clustering

Comparisons of the average degree of clustering between the homogeneous and patterned experimental landscapes revealed only minor differences in the number of ARS clusters and no differences in the size of these clusters and the time spent within them (figure 2), indicating that animals alternate intensive–extensive search behaviour irrespective of landscape features.

Strikingly, we found strong ARS clustering behaviour in both the homogeneous landscapes and in the bare areas of the patterned landscapes (figure 3a), strongly suggesting that the observed alternation reflects inherent behaviour of the snails, and therefore providing indications for intrinsic multi-scale search behaviour. On average, as much as 87–89% of ARS clusters in the random, regular and fractal landscapes were observed outside of food patches. Numbers are similar for time spent in search clusters outside of food (68–76%). Moreover, in the fractal and random landscapes, the size distribution of the ARS clusters outside of food patches was well described by a power law ($\mu = 1.8$; figure 3b and table 1b), which is again a clear signature of Lévy-like search behaviour [56]. Also, time spent in ARS clusters without food encounter was distributed with heavy tails in all landscapes (figure 3c), providing a direct parallel to earlier studies on intrinsic, multi-scale timing of search tasks [31]. Hence, we observed a large number of size- and time-diverse ARS clusters away from food patches, providing clear experimental evidence that the observed movement behaviour is inherent behaviour for our snails.

(c) Reaction to food encounter

Our observations that snails form search clusters away from food prompts the question whether they change their movement behaviour at all when encountering food patches. Despite the prominence of ARS clusters outside of food patches, we found that more than 90% of the encounters with food coincided with the start of an ARS cluster, clearly suggesting behavioural changes when animals encounter a food patch. Thus, snails seem to initiate local search both in the absence of food and in response to food encounter.

Additional analyses of patch arrival and departure directions showed that snails also often change search direction after exploiting food patches (figure 4). Turning angles between entry and exit of a food patch were centred on 180°, indicating that snails often reverse search direction within a food patch, exiting at a position not far from its entry point. On the contrary, turning angles (with an absolute value) below 90° appeared less frequently than at random, suggesting that at food encounter the previous course is lost. By strong turning behaviour, snails may try to exploit the food patch they just found [57]. These results indicate that snails, similarly to many other animals [58], react to the presence of food patches by initiating ARS, obviously trying to exploit them [5]. Thus, our results indicate that encounters with food (characteristic of the composite Brownian walks hypothesis) as well as internal triggers (characteristic of intrinsic multi-scale search behaviour) can initiate local ARS in the mud snails. The relative importance of each process depends on the density and spatial distribution of food patches.

(d) Search efficiency

Ecological theory proposes that Lévy walks are an evolutionary adaptation of naive foragers to optimize food encounter in

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Table 1. Parameters and test statistics of (a) two-dimensional move length distributions (see electronic supplementary material for one-dimensional distribution fit parameters) and (b) area sizes of ARS clusters outside of food patches, per landscape. x_{min} is the minimum move length/cluster size (obtained from a bilinear fit), w_{TPL} and w_{CBW3} are Akaike weights for the truncated power-law and hyperexponential fits with $k = 3$. G and D are the goodness-of-fit statistics of the G-test and the Kolmogorov–Smirnov test; for the latter, we provide a bootstrapped p-value. μ is the scaling exponent of the truncated power-law fit, OM is the order of magnitude over which this fit ranges, s_1, s_2 and s_3 are the characteristic scales of the exponential components of the hyperexponential distribution. Bold numbers indicate best fits; italics emphasize important scales and significant exponents. Fits to power-law, exponential and hyperexponential ($k = 2$) distributions were included in the analysis, but not listed here, because of poor results.

| landscape	x_{min}	w_{TPL}	G	D (p)	μ	OM	w_{CBW3}	G	D (p)	s_1	s_2	s_3
(a) move length distributions (mm)												
bare	1.1	0	−450.4	0.099 (0)	2.15	2.44	**1**	−63445.5	0.011 (**0.10**)	2.63	13.89	48.99
fractal	1.1	0	−494.0	0.097 (0)	2.15	2.44	**1**	−69595.8	0.014 (<0.01)	2.59	6.87	35.53
random	1.2	0	−632.8	0.080 (0)	2.59	2.51	**1**	−89138.2	0.013 (<0.01)	2.25	10.69	43.78
regular	1.3	0	−575.0	0.089 (0)	2.45	2.09	**1**	−80999.4	0.030 (<0.01)	2.53	7.14	25.87
complete	1.2	0	−645.1	0.099 (0)	2.31	2.31	**1**	−90876.9	0.011 (<0.01)	2.59	5.94	35.48
(b) cluster area size distributions (mm^2)												
bare	2.4	0.11	−15.0	0.099 (0)	1.50	4.22	**0.89**	−5.04	0.028 (**0.64**)	6.02	20.41	759.19
fractal	32.9	**0.96**	−1.3	0.091 (**0.19**)	1.82	2.16	0.02	−0.50	0.042 (0.80)	67.22	172.12	2415.49
random	6.9	**0.80**	−12.9	0.073 (**0.09**)	1.79	3.31	0.10	−5.79	0.031 (0.70)	11.93	28.19	178.81
regular	6.1	0	−11.7	0.122 (0)	1.63	2.40	**0.98**	−1646.25	0.029 (**0.87**)	6.10	21.65	163.25
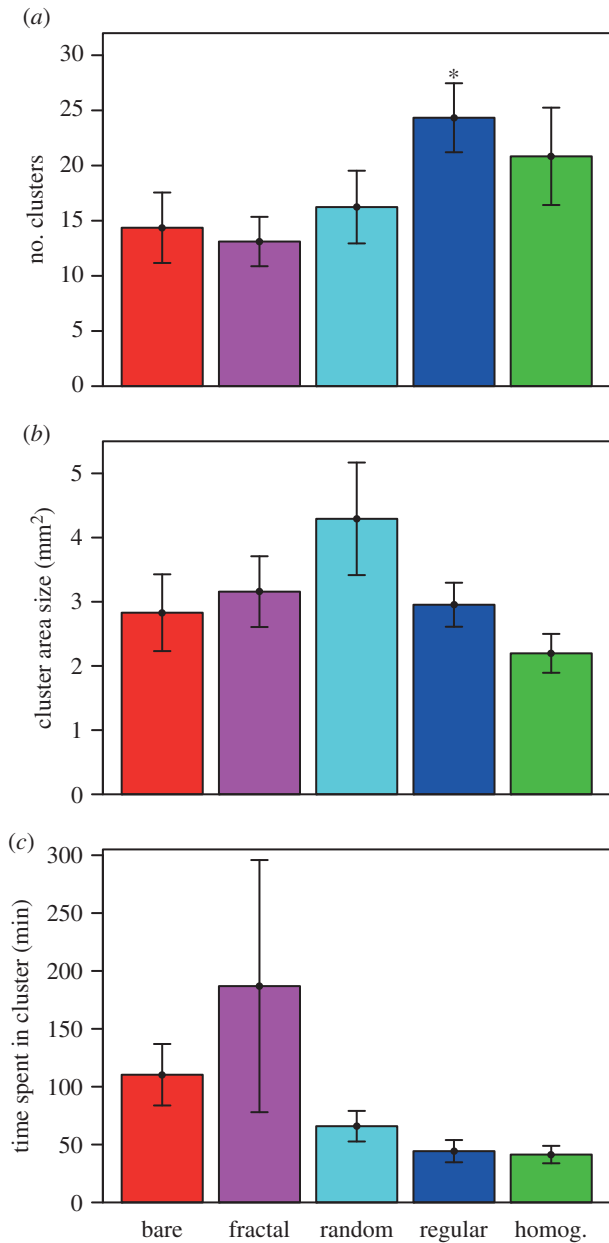
Figure 2. Cluster analysis results compared among the five experimental landscapes. (*a*) The average number of ARS clusters of individual tracks ($\pm$ s.e.) is significantly larger for the regular landscape (Wilcoxon tests, $p < 0.05$). In all other landscapes, snails produced similar numbers of ARS clusters, indicating that ARS cluster movement was not only initiated by food encounter. (*b*) Average cluster area sizes and (*c*) time intervals spent in the clusters for each individual ($\pm$ s.e.) reveal no significant differences among the landscapes. (Online version in colour.)

Figure 3. Cluster analysis results in relation to food encounter. (*a*) Proportion of ARS clusters on bare mud (light grey) and food patches (green; dark grey); see examples of search clusters on the right. Error bars are standard errors of the proportion of clusters on bare mud. (*b*) Cumulative inter-patch (i.e. off-food) cluster size distributions (tail) grouped by landscape type. Dashed lines indicate the best fit to each dataset; hyperexponential ($k = 3$) for the bare and regular landscapes, and truncated power-law for the fractal and random landscapes. (*c*) Cumulative distributions (tail) of time spent in inter-patch ARS clusters grouped by landscape. Dashed lines are best-fit hyperexponentials ($k = 3$) for all landscapes. Power-law scaling exponents are provided for all distributions; asterisks (only in (*b*)) indicate distributions for which power-law fits were superior to hyperexponentials. (Online version in colour.)

specific target heterogeneous conditions [1,29]. Our test of this hypothesis by using empirical survival functions of search efficiency (figure 5) showed that the time it took a snail to find food was affected by the food distribution (i.e. landscape type; Cox's proportional hazards model with covariates, likelihood ratio = 13.4, d.f. = 2, $n = 334$, $p = 0.0012$, Bonferroni-corrected threshold $p < 0.016$). Snails moving on fractally distributed food encountered patches faster than snails searching for regularly distributed food patches ($z = 3.8$, $p < 0.016$), revealing that the search efficiency of snails was highest in the experimental landscape most closely resembling their natural habitat [59]. Hence, our results suggest that multi-scale movement is not only the inherent search strategy for mud snails, but also the most efficient for finding food in the snails' native habitat configuration.
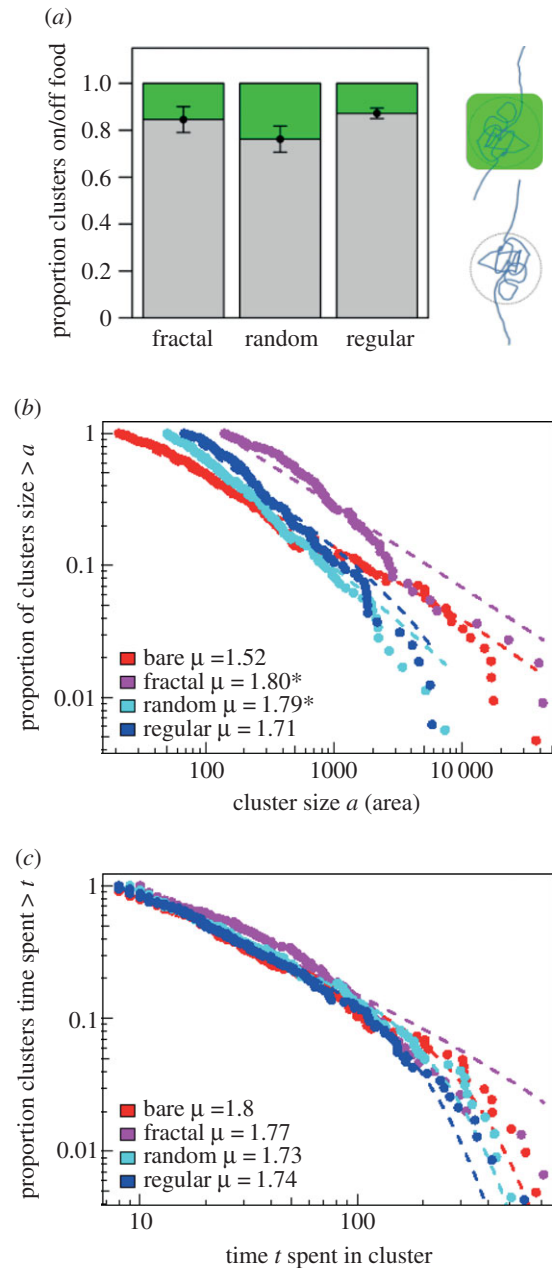
4. General discussion

In this work, we have put forward and applied a new experimental approach to test for the presence of inherent Lévy-like, multi-scale search behaviour, using mud snails that move as uninformed searchers in artificial landscapes and exposing them to different types of spatial food distributions. In all of our experiments, even in homogeneous landscapes, composite models consisting of multiple exponentials provided
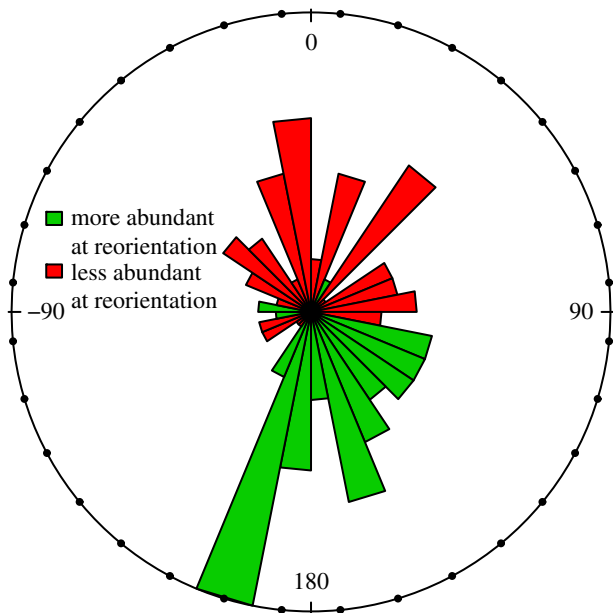
Figure 4. Reorientation at food encounter. Differences of abundances of turning angles between directions at food patch entry and exit and random turning angles of similar time lags. Green (light grey) indicates that at food encounter, the respective turning angles are more abundant than random, whereas red (dark grey) indicates that at the encounter of food patches, the angles are less abundant than random. This distribution differs significantly from a uniform distribution (Kolmogorov–Smirnov test, $D = 0.51$, $p < 0.001$). (Online version in colour.)

Figure 5. Survival curves representing the estimated proportion of individuals that have not yet encountered a food patch, for the three heterogeneous landscapes. Landscape type significantly affects time to first encounter (Cox's proportional hazards model with covariates, LR = 13.4, $p = 0.001$). (Online version in colour.)

the best fit to the overall movement, being superior to the fits provided by (truncated) Lévy walks. At first glance, this result supports the composite Brownian walk hypothesis [28], which explains long-tailed movement patterns by an alternation of Brownian movement modes triggered by external cues, such as food encounter or other environmental heterogeneity [8,29]. However, the general insensitivity of estimated parameters to the differing landscape features, in combination with the observation of clusters of ARS in homogeneous landscapes, contradicts this explanation. Close inspection of the search characteristics of mud snails in controlled landscapes revealed clear signatures of Lévy search behaviour: clusters of ARS were found in the (controlled) absence of food encounter, and the clusters followed a power-law size distribution. Thus, mud snails inherently switched between long-distance movement and area-restricted search, which reflects a multi-scale search strategy that is not solely triggered by the landscape.

Our finding of inherent complex movement strategies in mud snails is an important addition to the recent set of studies that aim at understanding the processes underlying multi-scale search patterns [23,27,31,32,36,60]. Similar to most of those studies, the timing of ARS clustering in mud snails showed multi-scale search behaviour also in a homogeneous environment, implying intrinsic behavioural control [31,34,36]. Because of our novel experimental set-up, we could also demonstrate spatial multi-scale foraging behaviour in the absence of food encounter [15]. Hence, and in accordance with other studies on search movement patterns in the absence of chemical cues [23], Lévy or more general multi-scale movement can be an intrinsic strategy of searching animals and does not require landscape heterogeneity or other external triggers as explanation.

Still, our results do not contradict the classical perspective on movement ecology where animals respond to environmental cues to make foraging decisions [2]. Search strategies
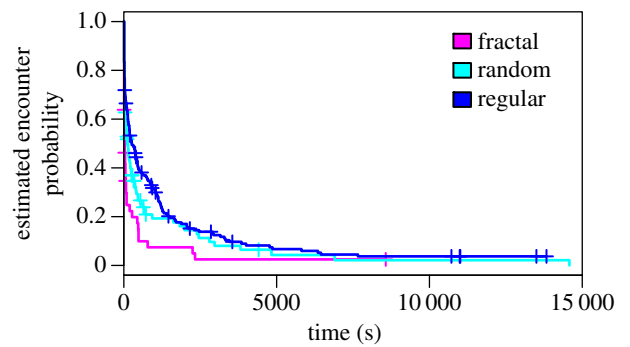
are per definition affected by encounters, as was shown in our study by the high percentage of food encounters coinciding with ARS clusters. Thus, observed movement patterns were modified by step truncation and increased turning. Analogously, we observed that in the regular and random landscapes, where encounter rates were highest, the Lévy exponent was increased relative to the bare and fractal landscapes to approach values that are more akin to Brownian motion. Thus, our findings contradict the hypothesis that long-tailed move length distributions are solely explained by animals adjusting their movement in response to food encounter or changing habitat characteristics [8,28,29]. Instead, we find support for the earlier-stated opposite hypothesis that Brownian motion may emerge from the interplay between inherent Lévy search behaviour and ecological encounters, such as consumption or interference, that lead to step truncations, especially in resource-rich or dense communities where ecological encounters are plentiful [30,55].

The result that mud snails were most efficient in finding food in fractal landscapes concurs well with the insight that diatoms are fractally distributed in the natural habitat of our mud snails [59,61]. However, the animals were still performing the same strategy in the other landscapes. Thus, these animals seem to have inherently followed a search strategy that is adapted to their environment, but probably robust enough to cope with other conditions, where, for example, food is distributed more homogeneously [30,62,63]. This insight supports the notion that Lévy and other multi-scale walks might be an evolutionary adaptation that provides a survival advantage if the environment is highly diverse [20] or changes [25].

One of our most striking findings is that the sizes of clusters of ARS can be described by power laws. To make sure that this is a valid conclusion for our data, we simulated tracks from truncated Lévy walks as well as composite Brownian motion and determined their cluster size distribution (see electronic supplementary material). The outcomes confirmed that power-law cluster size distributions are characteristic of Lévy walks. Cluster size distributions of composite Brownian motion were, on the contrary, best fitted by hyperexponentials. When disregarding fit quality, it was striking to see that we could fit any of the two simulated distributions (where parameters of our dataset had been used) with either a power-law or a composite Brownian model with similar parameters: (i) scaling exponents ($\mu = 1.68$ for the simulated Lévy and $\mu = 1.71$ for the simulated composite Brownian

motion) and (ii) hyperexponential parameters ($s_1 = 52 \text{ mm}^2$, $s_2 = 128 \text{ mm}^2$ and $s_3 = 503 \text{ mm}^2$ for the simulated Lévy, and $s_1 = 36 \text{ mm}^2$, $s_2 = 91 \text{ mm}^2$ and $s_3 = 538 \text{ mm}^2$ for the simulated composite Brownian motion). This indicates how very similar Lévy walks and composite Brownian walks are in supporting the concept of general multi-scale search behaviour, especially if composite Brownian walk parameters are carefully tuned [64]. Thus, we must be especially careful to not only fit distributions but, as we attempted, to find other means to test movement behavioural hypotheses [27,38].

Our investigation does not allow us to directly address the question about the underlying inherent process producing the multi-scale behaviour we found in our snails. The animals might follow an internal mechanism that approximates a theoretically ideal, random search process (e.g. the Lévy walk) [9,17,20,54,65] and that was carefully fine-tuned (see also simulations above) as an adaptation to optimize search strategies [55,64]. It was suggested that nonlinear processes in the brain might provide such a movement mechanism [31] and that inherent, characteristic macroscopic scales might govern them [36]. The latter are likely to exist for mud snails, because characteristic scales of the composite Brownian fits were similar for all landscapes; one scale even related to average snail body size. Another suggested mechanism, self-avoidance by inherent cueing [25], seems not to apply here, as tracks often overlapped, especially in ARS clusters.

The mud snails in this study alternated long moves with clusters of short moves and frequent turns even in the absence of external triggers such as food encounters. Alternations between movement modes of different scales in the absence of external triggers can be considered as a signature for inherent Lévy-type search strategies. Here, we view multi-scale search behaviour as a general movement strategy where the animal intrinsically alternates movement steps of different sizes, not in the mathematical sense of an observed precise power-law movement step distribution. To make a distinction between strict Lévy walks and biological implementations of Lévy-like patterns that are generated with different types of heavy-tailed distributions [15,33] and capable to optimize search, we propose for the latter to use the term 'multi-scale search behaviour'. In conclusion, our experiments provide an intriguing perspective on the behavioural processes that underlie search in foraging animals, and show new routes to explore the search problem of combining adequate experimental set-ups with simple quantitative approaches.

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